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THE GEOGRAPHICAL DISTRIBUTION OF CICINDELIDÆ IN EASTERN NORTH AMERICA.¹

BY CHARLES W. LENG,

WEST NEW BRIGHTON, N. Y.

INTRODUCTION.

My special interest in the tiger beetles dates from the time when Schaupp was writing his Revision in 1883, at which time I, as his pupil in German and entomology, was permitted to watch the progress of his work. That interest, always continued, received a special impetus from the publication of Professor Wickham's "Habits of American Cicindelidæ" in 1899, and I commenced to gather data in regard to habits and distribution and to view the subject from other standpoints than the purely taxonomic one from which my 1902 Revision was mainly prepared. With the advent of Dr. Lutz, considerations of the environment and evolution of our insects have been constantly kept before us, and have assumed an importance in our discussions that is largely responsible for the preparation of this paper. In the meantime also, the great work of Walther Horn which has been partly published in *Genera Insectorum*, the investigations of Norman Criddle and of Victor E. Shelford on the larvæ, the zealous collecting of Warren Knaus and others, have all tended to uncover hidden facts; and finally the untiring labors of our fellow member, Edward D. Harris, have culminated in the publication of his "Catalogue," in which the distribution of the species in his collection is minutely stated. So that it

¹ Annual Address of the President.

is now possible to give the complete distribution of our species with reasonable accuracy and to discuss the causes that have produced it. Such is the subject I shall attempt to treat in this paper.

TAXONOMY.

Before taking up the distribution of our species let me briefly sketch the classification and distribution of other Cicindelidæ in order to emphasize the small portion ours constitutes of the whole subfamily, for the Cicindelidæ are now regarded as merely a subfamily of Carabidæ. The subfamily is divided into five tribes, viz.: Ctenostomini, Collyrini, Mantichorini, Megacephalini, and Cicindelini, of which two, Collyrini and Mantichorini, are confined to the old world and do not at present concern us at all. A third tribe, the Ctenostomini, are confined to tropical climates, some species occurring in Yucutan, but none has so far come nearer to the southern limit of the United States. So that our interest centers in the tribes Megacephalini and Cicindelini. The former is represented by several South American genera, *Eucallia*, *Orychila*, *Chiloxia*, *Pseudorychila* and *Aniaria*, of which Mr. Harris has been kind enough to bring specimens for your examination. These genera extend for varying distances north of the isthmus of Panama, one reaching Honduras, another Costa Rica, but none attaining as yet the United States. The Megacephalini include also the species of *Omus*, confined to the Pacific Slope; the species of *Amblychila*, confined to the Sonoran region; and the species of *Tetracha* which are numerous, and covering nearly all the territory occupied by other members of the tribe, extend also beyond that territory and are found in the Antilles and in our southern states north to Cincinnati, Ohio, fide Dury, and Central Park, Long Island, where, as you know, a single specimen has been found by Mr. Davis. There remains to consider the fifth tribe Cicindelini; this, too, consists of several genera besides *Cicindela* proper, of which the South American *Euprosopus*, *Oxygonia*, *Odontochila* and *Prepusa* are represented in the box prepared by Mr. Harris of these genera. I know of no Central American species except *Odontochila* of which Mr. Harris has received a specimen taken in the state of Sonora, Mexico. *Cicindela* is therefore, though an important genus with us, only one genus in a large tribe and that tribe is only one of the five into which the subfamily is divided. The importance it assumes in our lists is greater than that to which it becomes entitled among the Cicindelidæ of the world.

Within the genus no proposed division has been generally accepted; but it is evident that two groups can be readily distinguished, the one containing the long-legged species in which the subapical margin of the elytra is often more or less emarginate and the mandibles more or less toothed, and the short-legged species in which such modifications of the elytra and mandibles do not occur. Other characters like the long labrum of *longilabris*, the form of the clypeus, and of the thorax, the pilosity and punctuation of the surface serve to separate species, but the important group character seems to me now to lie in the length of the legs. In the box, to which I have already referred, of South American forms you will see some of these long-legged forms which occur also in the West Indies, in Central America, in our Southern States, and represented by a few species even north to Massachusetts and Maine.

In concluding this brief reference to the different tribes and genera I wish to repeat and emphasize the northward procession of the family with numerous genera in South America, fewer in the Antilles and Central America, four only in the United States, with a corresponding procession of the long-legged species of *Cicindela*, diminishing in number northward, until *marginata* alone remains to represent them on the coast of Maine.

FACTORS CONTROLLING DISTRIBUTION.

Merriam's Zones.—Many considerations involving the causes of the distribution observed for different species of plants and animals have been advanced and each doubtless has its bearing upon the problem. The work of Merriam in defining certain zones based largely on the isothermal lines has been widely adopted as the exponent of the influence of temperature. In his pamphlet "Life Zones and Crop Zones of the United States" the Atlantic Coast is divided into tropical, gulf-strip, lower austral, upper austral, transition, and boreal. His map shows the meaning of these terms more plainly than any description I could give and you will note how irregular the lines become on leaving the coast, the colder zones descending far southward in the mountains, while the warmer zones, shown by yellow color, creep northward along the rivers like the Hudson and the Susquehanna. In the box I have prepared, colors corresponding to those shown on Merriam's map have been used to indicate the zones and

the specimens have been inserted in the zone within which they occur in nature. Each vertical line of specimens contains one species. At a glance you perceive how few species penetrate the boreal zone, indicating perhaps the inability of the others to live under its cold conditions; but you will also observe that the bulk of our species occur in several zones. Not always however without some modification in the different zones. Compare the dark *12-guttata* of Lakehurst, N. J., with the bright green specimen from Cape Breton, or the little *dorsalis* of Florida with the much larger specimen from Massachusetts, and you will realize the modifications that do occur. The most marked example is in *tranquebarica* and here the forms due apparently to climatic differences have received varietal names, the southernmost form being called *vulgaris-minor*, reduced in size and dark with narrow lines, the northernmost, *horiconcensis*, large, brilliant metallic, with broad lines. Again in *repanda* and *punctulata* you see instances of the contrary where the species unmodified live in several zones. Thus it is evident that the influence of temperature in controlling distribution and in modifying color is one of the factors but not the absolute and only factor.

Akin to temperature as controlled by latitude is temperature as controlled by elevation, but as the mountain slopes which produce the latter also introduce other conditions, the differences that have been observed between lowland and mountain forms of the same species cannot be surely ascribed to temperature. The modification of *6-guttata* described as *harrisi*, the modification of *longilabris* described as *oslari*, and other similar modifications apparently resulting from elevation can only be doubtfully referred to the influence of colder temperature; it may however be significant that a more brilliant color results equally from high latitude and high elevation. An interesting case, when sufficiently confirmed, may be found in *longilabris* in Newfoundland, which near the sea-level is dark bronze, but in the mountains of the west coast, as indicated by three specimens only, is bright green.

Leconte's Districts.—Leaving the question of temperature and latitude and the Merriam zones, all of which on the Atlantic coast mainly control distribution north and south, let us consider the ideas of Dr. Leconte, which while they did not disregard the evidently boreal character of many species and the southern limit to the distri-

bution of others, brought into much greater prominence the importance of the mountain systems as factors controlling distribution east and west. In the introduction to the "Coleoptera of Kansas and Eastern New Mexico" Leconte divided the United States roughly into four or five parts: one, Pacific, lying west of the Sierra Nevada; one, between it and the Rocky Mountains; one, central, between the Rocky Mountains and the Mississippi Valley, and one, eastern, itself feebly divided by the Appalachian range. The map illustrating his idea was printed in 1859 and allowances must be made for the imperfect data, due to its early date, upon which it was based in comparing it with Merriam's. To illustrate its bearing upon the known distribution of Cicindelidæ I would point out that the Pacific district is the exclusive home of the genus *Omus* and that every single *Cicindela* found there is either a species confined to that district or a named variety abundantly differentiated from its nearest relative east of the Sierra Nevada. The district between the Sierra Nevada and the Rocky Mountains is equally rich in peculiar forms. If it is true that the barrier created by the Sierra Nevada and that caused by the Rocky Mountains are factors in distribution, it should follow at least to some extent in the case of the Appalachian range. To test this I have arranged an east and west series of specimens of our *generosa*. A division caused by the Appalachian range is at once apparent. Observe that the middle band is always rectangularly bent in the specimens east of the Appalachian range, almost transverse in the western specimens which at the same time exhibit great variation in color. The names *formosa* and *manitoba* have been applied to them and to be consistent a name should be provided for our constant eastern modification. I have noticed the barrier constituted by the Appalachian range in other families resulting in slightly differentiated forms east and west and cannot but feel that Dr. Leconte's early ideas have been too long neglected. As the Merriam zones represent a factor operating north and south, the Leconte districts represent another operating east and west and with approximately equal force.

Environment.—Totally distinct from latitude and longitude is the factor of local environment, the character of the soil, its slope, the surrounding vegetation, moisture, exposure, etc. To remind you that *dorsalis* is always found on the seashore, *rugifrons* and *modesta* usually in the pine barrens is all that is necessary to illustrate the

importance of this factor; indeed its bearing upon problems of distribution is so evidently weighty that one is apt to question whether latitude has any influence except as it affects environment. In the case of *dorsalis*, itself a marked example of an insect clinging to one environment, I have already shown that while the beach sands are necessary to the creature's existence, and finding such sands along the coast from the Gulf of Mexico to Massachusetts, it has extended its range that far north, crossing four zonal boundaries in its northward journey, yet it has not preserved an unchanged identity in so doing but passes through the variations called *saulcyi*, *media* and *semipicta*. Conceding the great importance of environment, I must still maintain that like the factors previously considered it is only one of many affecting distribution.

In this connection I should point out the various observations of many collectors on the soil and other characteristics of the localities in which the different species occur. Locally it is well known that *dorsalis* lives on the sea beach, *hirticollis* and *lepida* on the looser sands back of the beach, the latter also on loose white sand inland, *marginata* on mud flats, all more or less maritime; while an entirely different set of species inhabit the sandy pine barren plains, *rugifrons*, *modesta*, *consentanea*, etc.; it is also known that while a species like *repanda* may be found in a variety of semi-moist situations, *12-guttata* can be expected only on the still more moist soil adjoining water and *purpurea* and *sexguttata* only on grassy hills or the latter in deciduous forests, at least locally. Each species in short seems to require a special environment and to insist upon it with a rigor that is in inverse proportion to its abundance.

Moisture.—In dealing with the distribution of the tiger beetles of our western states a special emphasis would have to be laid upon the influence of moisture; indeed in Dr. Leconte's division of the country into districts one is based upon the difference between the dry plains lying east of the Rocky Mountains and the more fertile country bordering the Mississippi River. Also in the same connection, the fauna of the saline lakes would require special consideration; but in the eastern parts of the United States, these matters do not present sufficient diversity to constitute important factors.

Behavior.—The meaning of these peculiarities has been traced back to the larval history of several species by Norman Criddle in

Manitoba and by Victor Shelford in Chicago. Showing first that the imago does not wander far from the larval home, Criddle has recorded patient investigations of the larvæ, describing the burrows they make in the soil, the nature and slope and moisture necessary for each species observed and the length of time passed in the larval and pupal stages. Shelford, repeating Criddle's observations, has studied the species living on the shores of Lake Michigan where varied conditions of slope, forest and moisture are found, and has determined experimentally the insistence of each species upon its customary environment. A female *limbalis* for instance, knowing that her larva will require sloping soil of a certain degree of moisture, will not oviposit in loose sand. A female *6-guttata* will oviposit only in what Shelford, following Cowles, calls climax forest, composed of beech, oak and other deciduous trees.

The bearing of these facts upon distribution is of great interest for if the female flies only from one suitable habitat to another, and cannot or will not fly to any great distance, it follows that any considerable interval of unsuitable soil will act as a barrier and retard the distribution of the species, even when suitable habitats exist beyond the barrier. If the intervening unsuitable territory is sufficiently extended, it may even serve to isolate the favorable habitat as completely as if it were an island in the ocean. This I conceive is the case in actual experience with *rufiventris* in the east plains of New Jersey. There with the adjoining west plains, which I have not seen but assume to be similar, is a peculiar piece of territory, in which Mr. Davis and I found gravelly hills about 100 feet above sea level in the midst of pine barrens. The very porous nature of the soil and its slope conspire to produce so dry a condition that ancient oaks are only 18 inches in height and the tallest pine tree we found was four feet in height. In this situation lives a species, *rufiventris*, not found elsewhere in New Jersey. Should the female wander from these hills to oviposit, she could not find a similar locality in the entire state and so year after year, century after century, *rufiventris* goes on inhabiting this small piece of the earth apparently a prisoner forever. The same appears to be the case with *hentzii* confined to certain dry hills in eastern Massachusetts and with some western species.

Adaptability.—With every other factor equal there still remains one that has evidently played an important part, *i. e.*, the adaptability

of the species to changing environment; *tranquebarica* and *longilabris* appear to have had a similar history, both driven far south during the glacial period, both returning northward with its retreat, both strong species represented by numerous varieties and abundant wherever they occur. But the one has survived the changing climate southward and continues to thrive in the austral zone as well as in the transition and boreal; while the other, *longilabris*, though it must have been driven far south of this latitude during the ice age, except on the probable assumption that it survived the ice age exclusively in isolated, northern, sheltered localities, has failed to survive even in the mountains and is now strictly confined to the boreal zone, having perished elsewhere as the temperature increased. The only cause I can imagine is that *tranquebarica* could and did adapt itself to the growing warmth of the Carolinas, Georgia and Louisiana and survives, while *longilabris* could not and so perished. It had the same chance but could not take advantage of it.

Accidents.—So powerfully deterrent to extended distribution is the influence of environment combined with the wilful behavior of the insects themselves that the marvel would be that many have spread so far were it not for the results of another set of factors that my friend Chas. R. Plunkett, who was with us at the last meeting, summarized under the name accidents, meaning thereby winds, currents, human interference, geological changes, anything acting independent of or contrary to the will of the insects. The widespread distribution of *punctulata*, flying as it does to lights at night and thereby exposing itself to the action of wind, and capable moreover of making itself at home in any garden path, is a case in point. The occurrence of *puritana* at widely separated points on the Connecticut River is another, for the gravid female could be carried as well by the river current in the one case as by winds in the other. In the case of our maritime species it is equally easy to conceive of the action of tides and storms providing the accidents that assisted in the dispersal of the species.

Dipping for a moment into the geological history of our continent we find readily enough stupendous accidents that must have profoundly influenced the distribution of our tiger beetles. I will refer however to but two, the glacial period and the former connection of this continent and Siberia.

During the glacial period everything on the Atlantic coast north of this latitude was covered with ice and snow and the climate immediately south of us must have been materially colder. Previous to the glacial period an opposite condition prevailed; the climate far to the north was temperate, forests flourished north of the present Alaska, and a comparatively warm British America was connected with an equally warm Siberia. The accidents of tide and wind and current, of elevation or subsidence of coastal plains, even of volcanic eruption are as nothing compared with the accidents to which tiger beetles were exposed before and during the glacial period. One can conceive of nothing to prevent the distribution of species from one continent to the other while they were connected. Even now we hear of circumpolar species, then each and every species may have been circumpolar in its distribution, displaying only such varieties from the opposite ends of its range as we find now in the *tranquebarica* of eastern and Pacific America. Then came the ice age, covering the north land with ice and snow, leaving possibly an always unglaciated area, as indicated in the map of Salisbury and Chamberlain, in Wisconsin extending northward into British America and perhaps other smaller unglaciated areas elsewhere, with alternating periods of extreme cold and milder climate, driving the tiger beetles south, then allowing them to return, then driving them south again, over and over again. At least three such alternations are traced by geologists. Need we be surprised if some species were exterminated and others nearly so? Would not naturally some survive the ice age as isolated remnants of a once far spreading species? And with the barriers I have indicated to their dispersal might they not to this day exist as isolated colonies? Compare with this theory the actual distribution of *ancocisconensis*, White Mountains of New Hampshire, De Bruce in Sullivan Co., N. Y., Cazenovia Creek near Buffalo, N. Y., and the mountains of West Virginia, four isolated stations with no localities known between. Compare *marginipennis* living on the mountainous banks of the Delaware River at Callicoon, N. Y., and the similar banks of the Susquehanna River in Pennsylvania. Compare *lepida* found in Manitoba, Nebraska and vicinity of New York City. All understandable as remnants of glacier tormented species but on no other theory that I have ever heard advanced.

Origin.—I do not mean to imply that for all the species men-

tioned a circumpolar distribution must be assumed as an original condition. In that respect I have especially in mind *longilabris*, *12-guttata* and *purpurca*, because each of these has an existing prototype in Siberia or Europe. On the contrary after considering many of our species as emigrants from South America, and others as survivors of former circumpolar forms, there remains a residue which indicate in their characters no close relationship with the species of other countries and must be regarded as originating with us, at least in comparatively recent time. Such is evidently the case with the genera *Omus* and *Amblychila*, both peculiarly our own and such also I conceive to be the case with those of our species which do not range far enough north to indicate original circumpolar relations or far enough south to indicate South American affinities. Such for instance as *rufiventris*, *hirticollis*, *ancociscoensis*, *marginipennis*, and surely *lepida* and *generosa*. It is as reasonable to assume a North American origin for some species as a South American for others and most unreasonable to assume that the one region could have originated all and the other none. This subject has been in my mind ever since a happy discussion in 1902 between Mr. Schaeffer, Dr. Horn and myself, in which Dr. Horn held strongly to the idea of a South American origin, undoubtedly true as to many but I am convinced not as to all.

In speaking of the origin of these species I do so in the sense of their contemporaneous origin from preglacial species of the same genus, delving into their comparatively recent history, rather than into the first appearance of the genus on our earth. The evidence afforded by the fossil Coleoptera of the Don beds near Toronto, in which I understand many species are or may be referred to existing genera, would not suggest that great structural changes have taken place in tiger beetles since the glacial epoch; and such similarities in maculation as we observe in the European *caucasica* and our own *hirticollis*, bearing in mind the former connection through Siberia, may even suggest that in color and maculation little change has taken place.

The assumption of a South American origin for part of the species, and of a circumpolar origin for the remainder, part of the latter attaining their present characters on this continent before the ice age, part roaming over this continent and Eurasia, would imply

either that the northern forms originated long ago from the South American and became entirely separated from them during or prior to the Tertiary period, or would suggest that the long-legged South American forms and their North American relatives actually constitute a separate genus of different origin and with other characters (as in the mandibles and elytra) to differentiate it from the true *Cicindela* of the old world with which our northern species are for the most part related. Such a division of the genus has in fact been made though not at present generally adopted. The distribution of *Cicindela*, thus restricted, would then be in harmony with that of many other genera of Carabidæ, the family of which the Cicindelidæ are now considered a subfamily.

Recapitulation.—I have now sketched and illustrated what I conceive to be the principal factors controlling distribution of Cicindelidæ on the Atlantic Coast, viz.:

Temperature as indicated by Merriam's zones,

Barriers as indicated by Leconte's districts,

Environment, etc., as brought out by Criddle, Shelford and others and including the behavior and adaptability of the species,

Accidents of wind, tide and geological changes, and

Original Habitat of the species. I propose below to examine the distribution of each species as given in Mr. Harris's Catalogue to see if the factors named are sufficient to account for the ascertained localities, dividing the species into three groups, viz., those assumed to be of circumpolar origin, those assumed to be long established in the United States, though originally derived from the same stock as the species of the first group, and those assumed to be of southern origin, mainly the long-legged species.

SPECIES OF CIRCUMPOLAR ORIGIN.

C. longilabris, including the varieties *laurenti*, *oslari*, *montana*, *vestalia*, *perviridis*, is strongly differentiated by the form of the labrum, a character it shares with the Siberian *silvatica*, which it also resembles in other respects. It inhabits the boreal zone from ocean to ocean, reaching 58° N. Lat. in British Columbia and on the Atlantic coast is found in Newfoundland, Nova Scotia, Maine, in the White Mts. and in the Adirondacks. It possesses great vitality and capacity for variation but seems quite unable to accommodate itself to the

warmer climate of the transition zone. It seems plainly a circum-polar species driven south by the glacier but returning immediately to the colder climate as the glacier retreated. Where it has been found by my friends it has been on hard beaten paths, on stony banks at some distance from water, on the road above tree line on Mt. Washington, on bare rocks at Mt. Desert, Maine. The great number of varieties into which it divides are in keeping with the idea of various colonies isolated at different times by the alternating glacial action and developed since glacial times in their present isolated homes. Its failure to establish a home in the Catskills for instance, over which it must have roamed at some time during the retreat of the ice, is accounted for by its lack of adaptability.

C. 12-guttata, distinguished from other species by its more depressed form, has also an allied species in the old world, and like *longilabris* occurs from ocean to ocean and extends north on the Atlantic Coast to Newfoundland, but unlike that species has become established also in the transition zone. Moist roads, damp low places, are its favorite habitats. This species may even be found in the upper austral zone where cold wet sandy roads with humus mixed afford suitable breeding places but does not ever become abundant.

Its distribution is readily accounted for on the same theory as that of *longilabris* with a greater adaptability to explain its wider range. The stronger differentiation of the Pacific variety of this and other species may be due to a separation caused by the Sierra Nevada even previous to the glacial period. The close relation between this species and *repanda* assumed by some authors seems to me erroneous. They differ in form and outline, in maculation, and remarkably in habits and distribution.

C. purpurca with its numerous varieties occurring in nearly every part of the United States and Canada is a puzzling complex, but is nevertheless soluble by the factors I have suggested. It is evidently capable of immense variation and adaptable to a variety of climates, though quick to respond to a change of climate by a change in color or marking. It has no extreme southern form nor any relative in South America but has its old world prototype. On the Atlantic Coast as variety *limbalis* it extends from Newfoundland south to West Point and Ramsey as Mr. Sleight showed us last season; as typical *purpurca* it flourishes in Connecticut, New Jersey and south

to the mountains of Georgia; as *transversa* it occurs in the same Georgia mountains and elsewhere in the south; in Maine it has developed a special form called *spretæ*. Westward it has split into many more varieties, of which most resemble the variety *transversa* more than typical *purpurca*, with the Pacific forms as usual more differentiated and more like the related old world species. Assuming an original circumpolar stock of which the Pacific branch retained the greater resemblance to the Siberian, while the Atlantic resembled the present *transversa*, all driven southward during the ice age, the Pacific branch would become isolated by the Sierra Nevada and develop the present Pacific forms, while the Atlantic form would survive in the most southerly point to which it was driven during the ice age, possibly the mountains of Georgia, spreading thence northeast and northwest and developing in the changing climates it reached the forms we now have. All the time the task of splitting the whole mass into isolated groups is being accomplished by the alternating northward and southward motion of the glacier's front. Extermination would be the result if the species, demanding as it does, only a sloping soil for its breeding place, were not adaptable to the last degree. That it is so is evident from the variety of climates in which it lives as well as from the recorded breeding places, sometimes grassy, sometimes bare, but always sloping ground. The especially remarkable feature is the great number of varieties, so great that many have never been named, the result I believe of the capacity each colony, isolated by glacial action, has possessed of adapting itself to local environment and perpetuating a modified form of the original stock.

C. repanda and *C. hirticollis* are also species which are almost reproduced in old world species; *hirticollis* extending from Maine to Florida on the Atlantic Coast and westward to California and Mexico. On Long Island and in Rhode Island the indistinctly marked form called *nigrita* by Abbott Davis occurs and in the southwest the Mexican *ponderosa*, almost indistinguishable, occurs; *repanda* also extends from Canada to Florida and spreads westward to almost every state in the union without important modifications even in color. Mr. Harris sees in these species, especially *repanda*, very ancient forms of *Cicindela* and, I may add, adaptable to various environments, which have interbred for so long a time that all the specimens reach an established neutral character.

C. tranquebarica, which on the Atlantic Coast extends from Newfoundland to Florida and westward across the continent presents a parallel case, minus the enormous development of varieties. Southward this species becomes dark, small, faintly marked, var. *vulgaris-minor*, northward brilliant, large, broadly marked, var. *horiconcensis*, northwesterly it becomes *obliquata* and in the Sierra Nevada it meets the fate of other species and splits into varieties of which some are still unnamed. Its history is similar to that outlined for *purpurca* but breeding in a variety of flat sandy places, it has followed the broad plains and isolation has been less potent.

SECOND GROUP.

C. generosa is a species which does not occur in the boreal zone nor in the lower austral, which has no near relatives in the old world nor in South America, with a distribution extending from southern New Hampshire through Massachusetts, Connecticut, New York and New Jersey, across the mountains in West Virginia, Ohio, Indiana and Illinois, thence running northwest to Manitoba, where a variety is developed and southwest to northern Texas developing another variety. As already pointed out a third variety unnamed is made by our eastern specimens. I cannot see anything in this history but a species indigenous to the region it now inhabits driven southward by the glacier but returning later to its old haunts, without a capacity for adapting itself to colder regions; otherwise it would accompany *tranquebarica*, further north and south than it actually does. *C. lepida*, *C. ancocisconensis*, *C. marginipennis*, *C. rufiventris* are also parallel cases but complicated by the rigorous requirements of the species in choosing breeding places so that they have failed to spread as widely from the post-glacial colonies of survivors.

C. 6-guttata again parallels the story of *generosa* and it remained for Casey to point out the constant difference in punctuation between eastern and western specimens (compare *tridens* Csy.).

C. patrucla and *C. unipunctata* present no points of difference except that their abundance in the mountains of Georgia again points to that locality as the latitude to which glacier-driven species reached in their southward movement; *patrucla* has a variety *consentanca* in the New Jersey pine barrens that occurs nowhere else in abundance,

except, perhaps, the similar pine barrens of Long Island, and possibly indicates with *rufiventris* the southern limit of a separate glacial period.

C. rugifrons, including *modesta*, *unicolor*, *nigrior*, *carolina*, *lecontei*, *obscura*, *scutellaris* and other unnamed varieties occurs on the Atlantic Coast from Massachusetts to Key West inhabiting sandy pine woods near the coast; and, avoiding the mountains, extends through the central district to Ontario and Manitoba, though much modified in the various parts of its range. The occurrence of the black *modesta* and the green *rugifrons* side by side in the same region is puzzling. It has been suggested that larval holes of different depth would expose the pupæ during the winter to different degrees of cold with a possible resulting difference in color of imago. I know of no proof that this is true. It may also be that the black forms and green forms became separated as a result of different glacial severities and have been perpetuated since. This question must remain unsolved until the origin of varying colors in tiger beetles is better studied.

SOUTHERN FORMS.

The species that remain are mainly of the long-legged group and fall into sections according to their habitats, which may be either pine woods of the coastal plain, marshes and mudflats, river banks or the shore of ocean and gulf. They resemble the long-legged species of the West Indies, Mexico and South America and several indeed are found south of our limits as *tortuosa* in West Indies, *hamata* in Mexico, etc. They can only be regarded as emigrants from the more southern countries and it is simply a matter of suitable environment and accident that determines how far north each shall extend.

Of the pine woods species, *striga* is confined to Florida, *hirtilabris* reaches northern Florida, *gratiosa* has been found as far north as Wilmington, N. C., by Messrs. Pollard and Engelhardt, *abdominalis* is abundant in summer north to Lakehurst, N. J., and may yet be found on Long Island. The roughly sculptured form *scabrosa* is however confined to Florida. Of the seashore species *dorsalis* with its varieties *venusta*, *sauleyi*, *media* and *semipicta* has now reached Cape Cod in Massachusetts, frequenting suitable beaches all along the coast southward to Florida, around it and along the

gulf coast to Mexico, always preserving its structural characters, but much modified in size. The marsh species are *severa*, which is confined to the gulf strip, *tortuosa*, which reaches Georgia, *hamata*, which, extending south to Mexico, does not get beyond the gulf states, and *marginata* which has reached Maine as evidenced by captures made by Mr. Harris this year.

Of the river species *blanda* is confined to Alabama and Georgia and is not yet known from Florida, the form cited by Leconte living on the Roanoke River in North Carolina may be identical; the closely allied *puritana* once considered a variety of *blanda* has been found last year by Mr. Davis in Maryland. It has been reported from New York but the locality is now unknown and its principal home as the name is intended to suggest is in New England on the banks of the Connecticut River.

Punctulata may also be included with these southern emigrants on account of its related Mexican forms. Being a strong flier and attracted by lights its wide dispersal has been an easier matter than that of the other species. On the Atlantic coast it occurs from Florida to Maine and inland it is found in most of the central and southwestern states. In those cases where southern species have traveled north along the Mississippi Valley they have become modified in entering the colder zone; thus *togata* becomes *apicalis* in Kansas, *blanda* develops into *macra* and *cuprascens*, but the majority have not gone in that direction but northward along the coast, the pine woods species aided by the almost continuous pine forests of the coastal plain, the maritime species by the tides and accidents of the sea.

SUMMARY.

In conclusion I hope I have shown you that if all the facts concerning geographical distribution of tiger beetles are not accounted for by the factors suggested, by far the greater part are so accounted for and there remain none at serious variance with the theories advanced. For the southern origin of many species the evidence is overwhelming, for the northern origin of others it seems to me nearly equally strong. Outside the question of origin, the bearing of latitude, longitude, environment and accident seem approximately equal in importance, each has undoubtedly played an important part in developing existing conditions.

To attempt to define zones or regions for such a group is a hopeless task for scarcely any barrier is effective for all the species, all the time; even the seas are crossed in the abundance of geologic time; the best one can do is to indicate the avenues of distribution the insects have followed, the sea beach, the river systems, the broad valleys and plains, along which some species have travelled further, some not so far, according to the adaptability of the organism to the new environments it has encountered, and the accidents that have assisted or retarded its progress.

Such avenues of distribution have been outlined in F. M. Webster's paper in *Psyche* on "Diffusion" and, though reached by entirely different reasoning, are not very different to those here suggested.

Turning to Mr. Harris's collection for a last look at *Tetracha* you may see what has happened to that genus—the most abundant of the tribe Megacephalini, represented in South America by numerous species, more capable of sustained flight than most, attracted to light, easily spreading through the mainland of Central America to Mexico, represented there by many species, with more difficulty crossing the seas between the West Indian islands and there represented by fewer species. Finally reaching the United States reduced to two species represented by numerous individuals in our southern states but until a few years ago, unknown northward. Then thanks to electric lights perhaps, it became abundant in Cincinnati. Last year, by Mr. Davis's fortunate capture, we learned that it had reached Long Island.

It is by accident that every beetle in Mr. Harris's box has its head pointed northward, but nevertheless it indicates, as truly as the magnetic needle indicates the pole, the direction in which these species are moving.



NOTES ON THE DISTRIBUTION OF SEVERAL SPECIES OF TIGER BEETLES.

BY WM. T. DAVIS,
NEW BRIGHTON, N. Y.

On June 28, 1911, Mr. Ernest Shoemaker and the writer, with some Washington friends, went to Chesapeake Beach, Md., in search